RESEARCH PAPER

Maintenance of an abrupt boundary between needle-leaved and broad-leaved forests in a wetland near coast

Shiro Tsuyuzaki[1], Akira Haraguchi[2]*

[1]Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan
[2]Faculty of Environmental Engineering, The University of Kitakyushu, Kitakyushu 808-0135, Japan

Abstract: There is an abrupt boundary between two well-developed wetland forests, a stand consisting of a broad-leaved, nitrogen-fixer *Alnus japonica* and a stand of the needle-leaved *Picea glehnii* Masters, in eastern Hokkaido, Japan. To clarify maintenance mechanisms, we studied the forest profile, water level, groundwater and precipitation chemistry, seedling establishment patterns in relation to microhabitats, and seed migration. The profile of groundwater level insufficiently explained the abrupt boundary formation, while the groundwater chemistry differed significantly between the two forests; i.e., EC, Na^+, K^+, Mg^{2+}, Ca^{2+} and Cl^- were higher in *P. glehnii* forest and pH was lower. Precipitation in *P. glehnii* forest contained richer Na^+, Ca^{2+} and Cl^-, indicating that the differences in surface-water chemistry were mostly derived from precipitation. Solar radiation was less than 2.2 $MJ \cdot m^{-2} \cdot d^{-1}$ on *P. glehnii* forest in late June, while that was patchily distributed in *A. japonica* forest with a range from 1.0 to 3.7 $MJ \cdot m^{-2} \cdot d^{-1}$. Moss cover on the soil surface, most of which were made of *Sphagnum* spp., was 60% in *P. glehnii* forest, but was 10% in *A. japonica* forest. Surface water chemistry represented by pH was considered to determine the development of *Sphagnum* moss. About 70% of *P. glehnii* seedlings < 1.3 m in height established on moss cover. Seed-sowing experiments suggested that seed germination and seedling survival for both species were significantly higher in *P. glehnii* forest. Therefore, the regeneration of *P. glehnii* in *A. japonica* forest was negligible, owing to the paucity of favorable microhabitats and low seedling establishment. *A. japonica* regenerated only by resprouting, and the seedlings were few in both forests. In addition, *A. japonica* seed migration into the *P. glehnii* forests was greatly restricted, and low solar radiation in the *P. glehnii* forest contributed to low seedling survival. Based on those results, we concluded that *Picea glehnii* and *Alnus japonica* could develop distinct and selfish environments being unsuitable for the other species and inhibit natural afforestation of another species each other by excluding invasion.

Keywords: *Alnus japonica*; microhabitat; *Picea glehnii;* positive feedback switch; precipitation chemistry; seed dispersal; wetland forest

Introduction

Plant community boundaries are classified into abrupt and gradual, based on plant community profiles (Hobbs 1986; di Castri and Hansen 1992; Wilson and Agnew 1992). Three major determinants for the formation of abrupt boundaries have been proposed: 1) intense disturbance, 2) sharp changes in environmental gradients, 3) interaction between dominant plants, and positive feedback switch by dominant species.

On the first determinant, areas with disturbance regimes support plant communities different from non-disturbed communities, and the boundary between communities is consistent with the disturbance margin (White and Pickett 1985). Periodic disturbances, such as floods, soil erosion and landslide, contribute to the formation of communities with abrupt boundaries (Roberts and Ludwig 1991; Duncan 1993). An abrupt boundary on *Nothofagus* forest in southern Chile is initiated and maintained by landslide, volcanic deposits and anthropogenic fire (Veblen 1985). On the second determinant, sharp environmental changes create abrupt boundaries and restrict ecotone development (Delcourt and Delcourt 1992). Gradual transition between communities is formed in less disturbed sites, e.g., in southern California annual grasslands and coastal sage scrub (Hobbs 1986). Gradual nutrient gradients promote plant community overlaps in Fynbos communities (Richards et al. 1997). When topography and/or substrate are uniform or change gradually in space, the first and second determinants can not explain the mechanisms on abrupt boundary formation. On the third determinant, 'positive feedback switch' is that dominant species in a community modifies the environments to win competitors via resource acquisition, i.e., light and nutrients (Wilson and Agnew 1992). For example, interspecific com-

petition between two dominant salt marsh plant species, *Salicornia* and *Arthrocnemum*, takes place in the boundary area, and a resultant sharp boundary develops (Pennings and Callaway 1992). In an experimentally-created freshwater marsh, competitive exclusion between two *Typha* species causes the formation of abrupt boundary (Grace and Wetzel 1981). If two communities contact and develop distinctive environments to exclude competitively to each other, then the abrupt boundary is developed.

The evergreen needle-leaved tree *P. glehnii* Masters and the deciduous broad-leaved tree *A. japonica* form wetland forests in Hokkaido, northern Japan (Tomizawa et al. 1997; Hotes et al. 2001; Haraguchi et al. 2003). On a flatland in eastern Hokkaido, *P. glehnii* and *A. japonica* forests contact and create an abrupt boundary. Clarifying the maintenance mechanism of the abrupt boundary between *P. glehnii* and *A. japonica* forests from natural deforestation and afforestation process of these two forests is the main objective of our research. The first and second determinants seemed not to explain sufficiently the boundary formation, since physical and topographical environmental changes are not clearly shown. We suspected that this boundary was formed by the third determinant. In particular, the two species have contrast and specific characteristics, i.e., *P. glehnii* produce acidic soil environment (Haraguchi et al. 2003) and *A. japonica* is a nitrogen-fixing plant. To confirm the mechanisms of the abrupt boundary formation, we surveyed the followings: (1) differences in forest structure and environmental factors, including water level and chemistry, between the two forests, (2) safe sites for the establishment of seedlings on *A. japonica* and *P. glehnii*, and (3) seed migration to the opponent forest.

Materials and methods

Study area

The study area is located in Hichiripp Mire (43° 04' N, 145° 00' E, 20 m a.s.l.), eastern Hokkaido, Japan in the cool temperate zone. Annual mean temperature is 5.9°C, and annual precipitation is 953 mm (Sakakimachi Weather Station, 15 km from the study site). Maximum snow cover thickness in this area is ca. 50 cm. Hichiripp mire locates at ca. 6 km from the Pacific Ocean, and then the precipitation is affected by sea salts in the atmosphere. Chemical property of the precipitation in the Kiritapp mire, near to the Hichiripp mire appeared in Tomizawa et al. (1997). Two forest communities were recognized: *P. glehnii* forest and *A. japonica* forest. The boundary between the two forests is abrupt.

Peat depth is more than 70 cm thick in the study area (Haraguchi et al., unpublished data). Below the peat, the bedding stratification of compacted peat, volcanic ash and sand is distributed widely in this region, because of several volcanic and tsunami deposits about 350 years ago (Nanayama et al. 2003). The position of the abrupt boundary has not changed for more than 30 years, confirmed by aerial photographs taken in 1967 and 1999. The sampling of tree core could not be made, because this *Picea glehnii* forest has been reserved as an official conservation area. The forest age can not be determined, but the largest *P. glehnii* tree in this forest was 64 cm in diameter at breast height

that was usually > 100 years. Small-scale selective logging was conducted in the past as seen by a few stumps near the study site, but was unlikely to have influenced the creation of the forest boundary. A 7-ha plantation of *Abies sachalinensis* was established 500 m from the study area in 1955.

Plant distribution patterns and topography

Five census lines separated by > 10 m were established perpendicular to the community boundary. Line 1 (85 m long) was set up in 2000, and the other four lines (Lines 2-5, 40–130 m long) were in 2001 to investigate the degree of overlap between the two communities. The measurement of diameter at breast height (DBH =1. 3 m high) was conducted on each stem in the years of the line setting. Trees ≥ 1.3 m in height located within 1 m of the lines were recorded by species, location and DBH using vernier calipers or a measuring tape. On *A. japonica* being frequently sprouting, main stem and each of sprouts > 1.3 m in height were measured on DBH. Based on binomial logistic regression, the position of boundary was determined on each line. On the regression, binary variate, i.e., *P. glehnii* or *A. japonica*, was used as dependent variable and the distance of each tree from the origin on the line was used as independent variable. When the divisive value is 0.5, we decided the boundary was overlaid on the point. Topography was measured by a transit compass (Ushikata, Tokyo) at 5-m intervals along Line 1. In the case to evaluate DBH-class distribution, the width of Line 1 was expanded to 10 m. All statistical analyses were made by SPSS ver. 12.0J.

Groundwater level

To investigate seasonal groundwater level fluctuations along Line 1, twelve vinyl chloride pipes (ϕ =3 cm, 1.3 m long) were inserted into the ground at 5 m intervals from the 15-m point to the 70-m point (Fig. 1). Two holes (ϕ = 5 mm) were drilled at 10 cm intervals on each pipe. The pipes were penetrated down to 1 m in depth. Groundwater level was measured by a ruler connected with a circuit tester. When the sensor was moved down slowly in the vinyl pipes and the electrical resistance changed greatly, the depth was regarded as the water level. Measurements were performed at two-week intervals during the snow-free period (May to November) in 2001. We examined linear, logarithmic, exponential and quadratic regressions to investigate the fluctuation pattern of water level along the line.

Solar radiation

To investigate the acquisition of solar energy ($MJ·m^{-2}·d^{-1}$) on the forest floor during seed germination duration, we set up 51 films for solar radiation measurement (OptLeaf R-2D, Taisei Chemical, Tokyo) on Line 1. Three films were set up at 5-m intervals from 0-m point to 80-m point. Each film was placed at 10 cm high from the ground surface horizontally using a small stick. Exposure duration was from 19 June to 25 June in 2002, when leaf flush was almost completed. Differences in mean and variance on solar radiation were examined between the two forests by ANOVA

with Levene's test.

Chemistry of groundwater and precipitation

Groundwater was collected between 15 m to 70 m points on Line 1 at 5-m intervals during the snow-free period (Fig. 1). Plastic bottles (500 ml, 10 cm deep) with holes (ϕ = 5 mm) at the sides and bottoms were inserted into 5 cm deep from the peat surface in mid-May 2001, and were left until the end of sampling (late October, 2002). Water accumulated in the bottles was immediately discharged. Then, water was collected from the bottles by using a syringe 30 min after discharge. Samples were placed in a -20ºC freezer or 5ºC refrigerator within 1 hr after the sampling. Electrical conductivity (EC) and pH were measured by portable EC meter (ES-12, Horiba, Kyoto) and pH meters (D-23, Horiba, Kyoto) in a laboratory. Samples for ion analysis were filtrated by a 0.20-µm nitrocellulose membrane filter (25AS020AN, Advantec Toyo, Tokyo), and then cations (NH_4^+, Na^+, K^+, Mg^{2+}, Ca^{2+}) and anions (Cl^-, NO_3^-, NO_2^-, SO_4^{2-}, PO_4^{3-}) were analyzed by an ion chromatograph (DX-120, Japan Dionex, Tokyo).
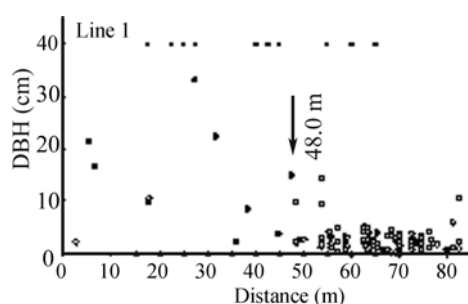
Fig. 1. Locations of trees > 1.3 m in height shown with stem diameter at breast height (DBH) along Line 1. Open arrows indicate the locations of boundary between *P. glehnii* and *A. japonica* forests. Solid triangles indicate the measuring points of groundwater level, and solid squares indicate the sampling points of groundwater. ●, *P. glehnii*; ○, *A. japonica*; △, Other species.

Stemflow was collected from stems wrapped by plastic gutters at 10–30 cm in height for *P. glehnii* and *A. japonica*, and was gathered in a plastic bottle placed under the gutters. Trees with a range between 10 cm to 30 cm at DBH were selected in and near Line 1. Samplings were made to 4 stems on each of the two species, and total sampling times were 16 times during 2 May and 28 October in 2002. At each sampling time, the water was collected when the amount of stemflow was enough to measure ions. The water samples were placed in a freezer at -20ºC immediately after the sampling. The procedures on the chemical analyses of stemflow were the same with those of groundwater. MANOVA was used to compare differences in the chemical characteristics between the stemflow of two species and between the surface water of two forests.

Distribution of stems in understory and forest floor

To estimate the regeneration status of *P. glehnii* and *A. japonica*,

stems < 1.3 m in height were measured in three 2 m × 2 m plots setting up at 5-m intervals on Line 1. The measurement was carried out between April and May in 2001 before current seedlings emerged. Based on morphological traits, regeneration type on each stem, i.e., seedling or sprouting, was checked. To evaluate regeneration safe sites, microhabitats were classified into three categories: moss cover (mostly by *Sphagnum* spp. and *Hylocomium* sp.), litter, and other, and the microhabitat type were recorded for each stem. Since the surface of *Carex* tussock was covered mostly with thick *Carex* litter, *Carex* tussock was assigned to litter microhabitat. In each plot, the outline of microhabitats was sketched on section paper with 10-cm accuracy, and microhabitat areas were measured on the sketches by a digital planimeter (Uchida Co., Tokyo). The relative dominance of each microhabitat was calculated based on the areas. χ^2-tests were used to investigate microhabitat preferences of *P. glehnii* seedlings in each forest.

Seed germination and seedling survival

To detect the effects of microhabitats on seed germination and seedling survival of *A. japonica*, 10 cm × 10 cm plots were set up in the two forest communities on 23 May 2001. In total, 39 plots were set up, and 18, 10 and 11 of them were, respectively, set up on moss cover in *P. glehnii* forest, litter in *P. glehnii* forest and 11 on litter in *A. japonica* forest. Seeds were collected from *A. japonica* forests 10 km from the survey area in autumn 2000, and refrigerated at ca 5ºC until use. In each quadrat, one hundred seeds were sprayed uniformly, i.e., the seeds were separated by about 1 cm from each other. Each seedling was marked by a small flag when the seedling was emerged, and the survival was monitored until leaf fall began in mid-October, 2001. In 31 August 2002, reinvestigation of the seedling survival was conducted.

For *P. glehnii* forest, 10, 18, 5 and 12 plots were set up on moss cover in *P. glehnii* forest, litter in *P. glehnii* forest, moss cover in *A. japonica* forest, and litter in *A. japonica* forest, respectively, at 24 April 2002. *P. glehnii* seeds were collected from a *P. glehnii* plantation 40 km from the study area in autumn 2001, and refrigerated at ca 5ºC until use. The monitoring was continued until 4 October 2002. The less numbers of plots on moss cover in *A. japonica* forest were owing to the paucity of moss cover in the forest. Two-way ANOVA was used to investigate the differences of seed germination and seedling survival between microhabitats and between forest types on each species.

Seed dispersal

Fifteen 0.25 m² seed traps were placed at 70 cm above the ground surface along Line 1 (Fig. 1). Monitoring began on 4 October 2000 before *A. japonica* and *P. glehnii* dispersed seeds, and finished on 18 April 2001 when the seed dispersal ceased. A preliminary survey confirmed that the two dominant species, *A. japonica* and *P. glehnii*, dispersed the vast majority of their seeds during this period. Linear, logarithmic, exponential and quadratic regressions were applied to investigate the relationship between locations and number of seeds captured.

Results

Forest physiognomy and boundary

Binomial logistic regression indicated that the boundary established clearly at 48.0-m point on Line 1 (Fig. 1). In the figure, *P. glehnii* stems were distributed in the left side and *A. japonica* stems were in the right side. Hereafter, we called *P. glehnii* forest to positions between 0.0–m to 48.0–m points and *A. japonica* forest to the remainders on Line 1. The canopy layers in *P. glehnii* forest were 16–20 m while those in *A. japonica* forest were 5–7 m. The canopies were completely occupied by the two species (Fig. 2). On Lines 2, 3 and 5, there were no overlaps between the stems of *P. glehnii* and *A. japonica*. Even though the two species overlapped the distributions on Line 4, the canopy layers of the two forests were clearly separated. Therefore, we concluded that this boundary was categorized into abrupt type. *Abies sachalinensis* Masters stems, which should immigrate from the plantation, were sparsely distributed in all areas, and were small at < 6 m in height. Broad-leaved tree species, *Fraxinus mandshurica* var. *japonica* Maxim*., Fraxinus lanuginosa* f. *serrata* Murata*, Sorbus commixta* Hedl*., Prunus sargentii* Rehder*, Acer ukurunduense* Trautv. et Mey*., Acer mono* Maxim. and *Betula ermanii* Cham. occurred on the surveyed lines. All broad-leaved trees showed DBH < 20 cm, and the total relative dominance of basal area was 5%. A shrub species, *Hydrangea paniculata* Sieb., established well in the understory of *A. japonica* forest.
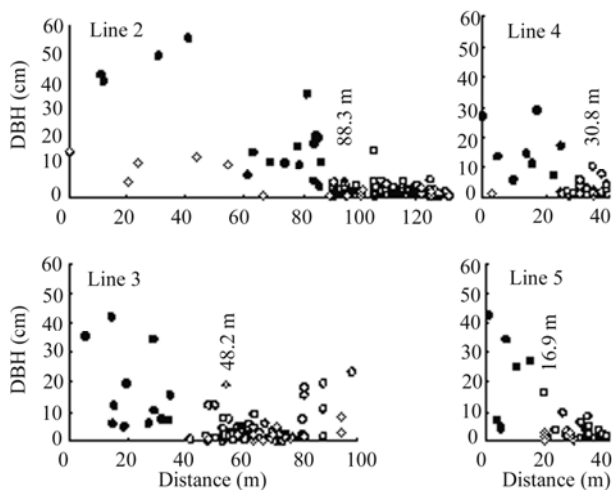
Fig. 2 Frequency distribution of DBH classes for *Picea glehnii* and *Alnus japonica* stems in *P. glehnii* and *A. japonica* forests

Relationship between DBH and tree height of *P. glehnii* and *A. japonica* on Line 1 in the Hichiripp mire showed that the saturated tree height of *P. glehnii* and *A. japonica* were 20 m and 6.0 m, respectively (Fig. 3). DBH of *P. glehnii* was 55.4 cm in the five lines surveyed, and DBH-class distribution showed that number of stems gradually decreased with increasing DBH (Fig. 4), suggesting that the regeneration of this species in *P. glehnii* forest have not stagnated. Most stems on the two species established in the opponent forests were located close to the boundary (Fig. 2).

P. glehnii established in *A. japonica* forest was shorter than the canopy layer of *A. japonica* forest. The maximum DBH of *A. japonica* was 23.2 cm. About 55% of *A. japonica* stems produced sprouts > 1.3 m high, and most *A. japonica* produced sprouts even if the sprouts were small. *A. japonica* established in *P. glehnii* forest was completely conducted by sprouting.
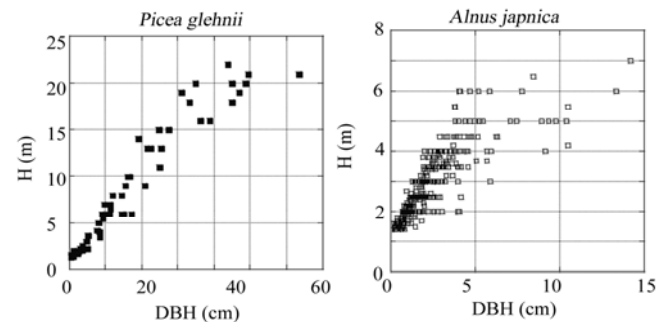
Fig. 3 Locations of trees ≥ 1.3 m in height shown with stem diameter at DBH along Lines 2 to 5. Symbols, see Fig. 1.
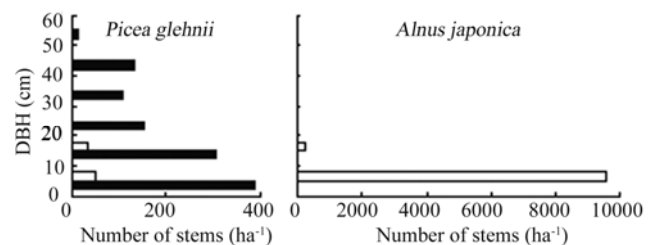
Fig. 4 Distribution of DBH and stem height of *Picea glehnii* and *Alnus japonica*.
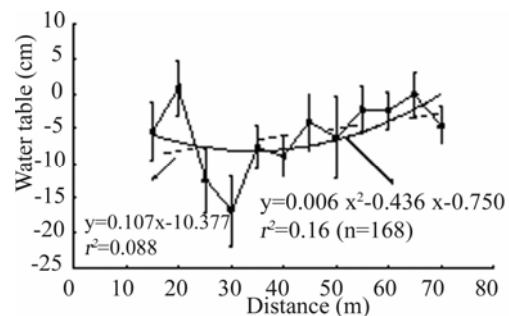
Fig. 5 Mean ground water level at 5-m intervals along Line 1 during the growing season. Bars indicate mean with standard deviation (*n* = 14). The fitted quadratic curve shown by a solid line explains change in water level more than the fitted straight line shown by an interrupted line.

Environmental variables

Topography was almost flat, and the difference between maximum and minimum elevation was 56 cm on Line 1 of which length was 85 m. Within 30 m of the boundary the elevation difference was < 16 cm. Mean groundwater level ranged from -16.8 cm to 0.8 cm (Fig. 5). Quadratic regression was fitted best to show the relationship between positions on the line and water level rather than linear regression. The quadratic regression in-

dicated that the groundwater level was lowest on the 30–35 m from the origin of Line 1. The position of the lowest water level was not consistent with that of the boundary, i.e., 48-m point (Fig. 1), indicating that the water level did not directly determine the boundary formation.

Groundwater pH ranged from 4.58 to 5.76, and was significantly lower in *P. glehnii* forest than in *A. japonica* forest (Table 1). EC ranged from 2.52 mS/m to 18.35 mS/m, and was significantly higher in *P. glehnii* forest. Of three nitrogenous compo-

nents, NO_2^- was nearly under detection limit in the two forests, NO_3^- and NH_4^+ were not significantly different between the two forests. Those suggested that nitrate in groundwater was not prime determinants on the forest differentiation. In total, four cation concentrations (Na^+, K^+, Mg^{2+} and Ca^{2+}) were significantly higher in *P. glehnii* forest. Cl^- was also higher in *P. glehnii* forest. PO_4^{3-} was always under detection limit on the surveyed line, and SO_4^{2-} was not significantly different between the two forests.

Table 1 Mean values with standard deviation on chemical properties of groundwater in *P. glehnii* and *A. japonica* forests and of stemflow of *P. glehnii* and *A. japonica* trees. The significant differences are confirmed by MANOVA. Asterisks indicate significant differences between groundwater in *P. glehnii* and *A. japonica* forests and between stemflow of *P. glehnii* and *A. japonica*, obtained by MANOVA (P < 0.01). *n*: number of samples collected. The units of anion and cation are mg·L⁻¹.

Item	pH	EC (mS/m)	NH₄⁺	Na⁺	K⁺	Mg²⁺	Ca²⁺	Cl⁻	NO₂⁻	NO₃⁻	PO₄³⁻	SO₄²⁻
Groundwater												
P. glehnii forest (*n* = 76)	5.2 ± 0.3	5.84 ± 2.85	0.7 ± 1.0	4.2 ± 1.0	1.4 ± 1.9	0.7 ± 0.4	1.5 ± 0.8	7.2 ± 6.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.9 ± 0.8
A. japonica forest (*n* = 38)	5.4 ± 0.2	4.14 ± 1.39	0.6 ± 0.7	3.5 ± 0.5	0.5 ± 0.4	0.4 ± 0.2	0.9 ± 0.4	4.4 ± 2.6	0.0 ± 0.1	0.2 ± 0.3	0.0 ± 0.0	0.6 ± 0.5
Significance	*	*		*	*	*	*	*				
Stemflow												
P. glehnii stem (*n* = 43)	4.4 ± 1.9 [1]	7.91 ± 7.07 [11]	1.4 ± 1.8	5.7 ± 4.2	4.4 ± 2.2	1.0 ± 0.8	4.0 ± 3.0	13.2 ± 15.3	0.1 ± 0.1	0.1 ± 0.2	0.3 ± 0.5	4.9 ± 3.5
A. japonica stem (*n* = 40)	5.1 ± 0.9 [1]	3.73 ± 2.76 [5]	0.6 ± 0.9	2.3 ± 2.4	5.5 ± 8.0	0.7 ± 0.8	2.1 ± 2.4	5.5 ± 7.9	0.2 ± 0.4	0.2 ± 0.5	0.1 ± 0.3	1.9 ± 1.8
Significance	*	*		*			*	*				*

[1, 5, 11]: each superscript numeral indicates number of samples not being measured, due to small amount of samples.

The differences of pH and EC in stemflow between the two species were broader than those of groundwater (Table 1). On pH, for example, *P. glehnii* stemflow pH averaged 4.4 that was significantly lower than *A. japonica* stemflow pH, 5.1. Difference in averaged groundwater pH between the two forests was 0.2, while that in stemflow was 0.8. The tendency of difference in EC was roughly similar with that of pH. The stemflow pH was lower than groundwater pH in both the forests. The concentrations of Na^+, Ca^{2+} and Cl^- those were significantly higher in groundwater were also higher in *P. glehnii* stemflow than in *A. japonica* stemflow, while K^+ and Mg^{2+}, being different in groundwater, were not significantly different. In particular, the three ions, being significantly different, in *P. glehnii* stemflow were 2-3 fold of *A. japonica* stemflow. The concentration of SO_4^{2-} in stemflow was significantly higher in *P. glehnii* stemflow, although that was not different in groundwater. Haraguchi et al. (2003) showed that throughfall as well as stemflow in *P. glehnii* forest in Ochiishi mires were acidic compared as bulk deposition. Sea salt concentration also showed similar tendency, and then acid in precipitation as well as released H^+ by cation exchange in peat soil would acidify soil in *P. glehnii* forest. Precipitation in *A. japonica* forest in the Kiritapp mire was not acidic (Tomizawa et al. 1997), and then throughfall and stemflow would be one of the cause of soil pH difference between *P. glehnii* and *A. japonica* stands in the Hichiripp mire.

Solar radiation during the germination period ranged from 0.8 to 3.7 MJ·m⁻²·d⁻¹ (Fig. 6). The fluctuation patterns of solar radiation changed sharply on the boundary. The solar radiation in *P. glehnii* forest was less than 2.2 MJ·m⁻²·d⁻¹ with an average of 1.4 ± 0.4 MJ·m⁻²·d⁻¹ (mean ± standard deviation). The mean solar ra-

diation in *P. glehnii* forest was significantly lower than that in *A. japonica* forest (2.3 ± 0.8 MJ·m⁻²·d⁻¹, range = 1.0-3.7). The difference in variance of mean solar radiation was significantly different between the two forests (P < 0.05), suggesting that solar radiation was highly variable in *A. japonica* forest. The lowest solar radiation in the two forests was not greatly different, while the highest value in *P. glehnii* forest was 60% as high as in *A. japonica* forest. Those indicated that the solar energy on the ground surface was totally low in *P. glehnii* forest, and was heterogeneously distributed in *A. japonica* forest.
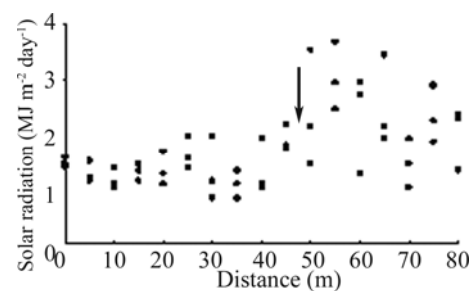

Fig. 6 Average solar radiation on the ground surface of two forests during June 19 2002 to June 25 2002. Open arrow indicates the boundary between *P. glehnii* and *A. japonica* forests.

Distribution of stems < 1.3 m in height

The relative dominance of microhabitats was significantly different between *P. glehnii* and *A. japonica* forests (Fig. 7). In *P. glehnii* forest, more than half of ground surface was covered with

moss, and litter microhabitat followed moss cover. In *A. japonica* forest, 85% of the ground surface was covered with litter that was mostly supplied from sedge tussocks, and moss cover was 15%. The other microhabitats were mostly occupied by woody substrata such as fallen logs, but were less abundant.
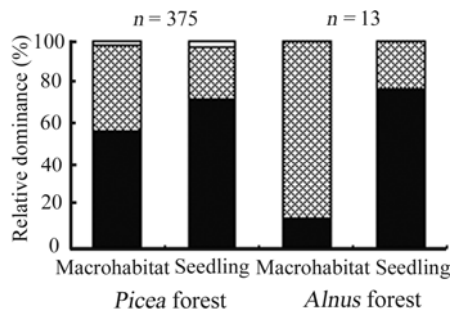
Fig. 7. Relative dominance (%) of microhabitats and *Picea glehnii* trees ≤ 1.3 m in height in *P. glehnii* and *A. japonica* forests. Microhabitat: closed = moss, dotted = litter, open = others. The differences in relative dominance between microhabitats and seedlings in the two forests and between microhabitats and seedlings are significantly different at P < 0.01 (x^2-test).

In total, 375 *P. glehnii* stems < 1.3 m high were recorded on 30 of 2 m × 2 m plots on *P. glehnii* forest, and averaged 3.1 stems m^{-2}. In 21 plots on *A. japonica* forest, 13 *P. glehnii* stems were found (0.2 stems·m^{-2}). All *P. glehnii* stems did not produce vegetative organs, such as sprouts, indicating that those regenerated from seeds. In contrast, all *A. japonica* stems were originated from sprouts. Therefore, all *A. japonica* stems in *P. glehnii* forest were located close to the boundary (Figs. 1 and 2). In *A. japonica* forest, seedlings and saplings of the other tree species were also few, indicating that seedling regeneration was difficult in *A. japonica* forest for most tree species.

Not only in *P. glehnii* forest but also in *A. japonica* forest, *P. glehnii* stems < 1.3 m in height favored to establish on moss cover (Fig. 7). The multiplier effect of habitat preference on *P. glehnii* and the paucity of moss microhabitat in *A. japonica* forest seemed to result in the restriction of *P. glehnii* regeneration in *A. japonica* forest.

Seed germination and seedling survival

To clarify the characteristics of earlier-growing stages for the two species, seed-sowing experiments were conducted (Fig. 8). For *P. glehnii*, the effects of microhabitats did not differ on seed germination and seedling survival, while the forest types affected the seedling survival but did not affect seed germination. Based on the seed-sowing experiments and the densities of *P. glehnii* stems < 1.3 m in height (Fig. 7), we concluded that *P. glehnii* seedlings could not survive in *A. japonica* forest, even though seed germination was not restricted.

For *A. japonica*, forest types did not affect the seed germination and seedling survival. On the microhabitats, differences in microhabitats did not affect seed germination, but moss microhabitat was the most favorable site for the seedling survival. Even if *A. japonica* seeds were supplied plenty, this species could regenerate

on moss cover. However, the moss cover was not enough to provide the regeneration in *A. japonica* forest, and the seeds did not immigrate into *P. glehnii* forest (see below).
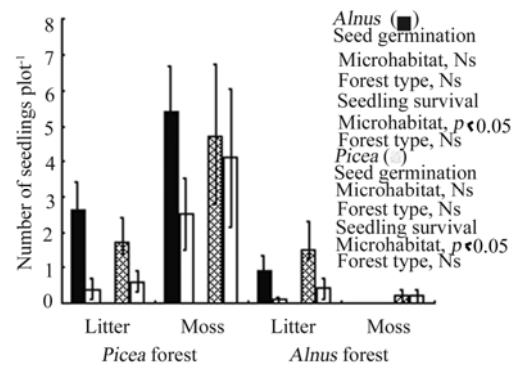
Fig. 8. Seed germination (closed = *A. japonica,* dotted = *P. glehnii*) and seedling survival (□, corresponding to left columns) of *A. japonica* and *P. glehnii* in two major microhabitats (moss and litter) in the seed-sowing experiment. Bars indicate standard deviations. All interactions between microhabitats and forest types on MANOVA are not significant.

Seed dispersal

Averaged total seed density captured by the seed traps was 911 seeds·m^{-2} during the surveyed period. Of those, 48% came from *Betula* spp., and 46% were from *Alnus japonica*. *Betula* seeds immigrated mostly from the adjacent area, since there were no reproductive *Betula* trees in the study area. No *P. glehnii* seeds were trapped throughout the surveyed period, probably because of non-masting. Linear regression was applied best to express the relationship between the positions of Line 1 and number of *Betula* seeds captured, while exponential regression was applied to the relationship on *A. japonica* (Fig. 9). These results implied that seed migration of *A. japonica* into *P. glehnii* forest sharply decreased at or around the boundary. The height of *A. japonica* canopy layer producing most seeds was less than 7 m (Fig. 2). The physical barriers such as forest structure of *P. glehnii* that inhibits seed migration from the flank may be related to the protection of the seed migration.
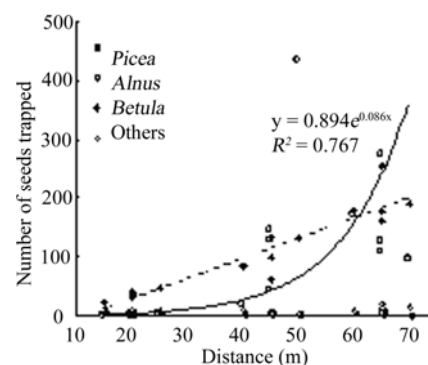
Fig. 9. Number of seeds captured by seed traps along Line 1, from 4 October, 2000 to 18 April, 2001. The best fitted lines for *Alnus japonica* and *Betula platyphylla* var. *japonica* are shown by solid and interrupted lines, respectively.

Discussion

The persistent boundary between *P. glehnii* and *A. japonica* forests is categorized into an abrupt type. The topography was flat, and groundwater level could not sufficiently explain the location of the abrupt boundary, suggesting that the physical environments were not the prime determinants on the boundary formation.

Sharp changes in chemical environments such as surface water chemistry often determine the distribution patterns of wetland communities (Vitt and Chee 1990; Haraguchi 1992; Keddy 2000). Water chemistry differed greatly between the two forests. pH was lower and EC was higher in *P. glehnii* forest than in *A. japonica* forest, and the concentration of all ions showing significant differences between the two forests were higher in *P. gle hnii* forest. Needle-leaved tree species often provide acidic stemflow (Cantu Silva and Gonzalez Rodriguez 2001). Sulfate reduction is related to acidification, and SO_4^{2-} was rich in the stemflow of *P. glehnii*. Stemflow pH is around 4.0 in a *Picea glehnii* coastal wetland forest, eastern Hokkaido (Haraguchi et al. 2003). For reference, stemflow pH is 5.4 in an *A. japonica* wetland on Kiritapp Mire near the study area (Tomizawa et al. 1997). The stemflow of *P. glehnii* contained rich ions, in particular, Na^+, Ca^{2+} and Cl^-. Those ions are supplied from seawater when wetlands are located adjacent to sea (Haraguchi et al. 2003). The canopy height of *P. glehnii* could capture more sea fog than that of *A. japonica*. Throughfall transmits more than 80% of precipitation-borne solutes (Parker 1983). However, the most of chemical properties showing significant differences between the stemflow of *P. glehnii* and *A. japonica* were also different between the groundwater of the two forests, indicating that not only throughfall but also stemflow greatly affected nutrient status in groundwater.

Chemical properties in water have relevance to the distribution of mosses and herbs in various wetland communities (Keddy 2000). In particular, the occurrence of *Sphagnum* is related to groundwater chemistry (Vitt and Chee 1990; Gunnarsson et al. 2000), i.e., *Sphagnum* mire tends to develop more on areas with lower pH (Wolejko and Ito 1986). Two *A. japonica*-dominated wetlands near the study area were in contrast with *Sphagnum* establishment and groundwater pH, i.e., *Sphagnum* established with pH < 5.5 (Hotes et al. 2001) and *Sphagnum* not established with pH ranged from 6.1-6.3 (Tsuyuzaki et al. 2004). These indicate that *P. glehnii* forest was more suitable for the establishment of *Sphagnum* than in *A. japonica* forest.

Three essential nutrients, N (NH_4^+ and NO_3^-), P (PO_4^{3-}) and K (K^+) were less or zero in the groundwater on the two forests. The concentrations of those ions were lower in groundwater than in stemflow. However, tussock-forming sedges often establish in *A. japonica* forests (Nakamura et al. 2002; Tsuyuzaki et al. 2004), probably because *A. japonica* is nitrogen-fixing plants. Those results suggested that those nutrients decreased primarily by plant consumption rather than diffusion in the ground. Light on the ground surface of *A. japonica* forest should be enough to develop herbaceous layers, although the light distribution was patchy.

Microhabitats often determine seed germination and seedling survival (Titus 1990; Tsuyuzaki et al. 1997; Keddy 2000).

Seed-sowing experiments showed that the effects of microhabitats on seed germination for *A. japonica* and *P. glehnii* were not significantly different. Seedling survival of *P. glehnii* was also not related to microhabitats. Microhabitat was related only to seedling survival of *A. japonica*, while forest type affected seedling survival on *P. glehnii*. These results meant that *A. japonica* seedlings could regenerate if the seeds were supplied enough to *P. glehnii* forest. However, a few *A. japonica* seeds immigrated into *P. glehnii* forest. Wind effect is found at short distance for the wind-dispersal seeds of *Cortaderia selloana* in Mediterranean wetlands (Saura-Mas and Lloret 2005). In the closed canopy of forests in the Hichiripp mire, immigration of seeds by wind would be limited because of the low velocity of wind in forests. In addition, the floor of *P. glehnii* forest is dark throughout the year, because of evergreenness. *A. japonica* species generally need high solar radiation for survival and growth (Walker and Chapin 1986; Haeussler and Tappeiner 1993), and the stem diameter growth of *A. japonica* is correlated to total sunlight over the growing season (Haraguchi et al. 1999). Naturally-regenerated *A. japonica* seedlings were least even in *A. japonica* forest, suggesting that solar energy was not enough for *A. japonica* seedling regeneration. Even if sufficient seeds were dispersed into *P. glehnii* forest, therefore, *A. japonica* seedlings could not survive under the canopy with low light intensity. *A. japonica* regeneration is mostly conducted by sprouting on frequently water-logged area in Kushiro Mire, eastern Hokkaido (Nakamura et al. 2002). Due to the sprouting habit, the expansion of distribution is restricted.

The most favorable microhabitat for naturally-regenerated *P. glehnii* saplings < 1.3 m high was moss cover. The sowing-experiment showed that seedling survival of *P. glehnii* seedlings was higher in *P. glehnii* forest. The moss cover in *P. glehnii* forest should be the best site for the regeneration of *P. glehnii* seedlings.

P. glehnii regenerates by seedlings that prefer to moss cover that is distributed mostly in *P. glehnii* forest, while *A. japonica* regenerates by sprouting to avoid low solar radiation on the ground surface. The development of moss cover is promoted by stemflow of *P. glehnii*, and is restricted by the development of tussocks in *A. japonica* forest, probably because *A. japonica* is nitrogen-fixing plant. In addition, the seed migration of *A. japonica* into *P. glehnii* forest was prohibited. By the integration of those effects, the abrupt boundary is maintained. The trigger of the development of the abrupt boundary is dependent on the individuality of the two species, i.e., stemflow and throughfall of *P. glehnii* vs nitrogen fixing by *A. japonica*.

'Positive feedback switch hypothesis' is that an abrupt boundary is developed when strong inter-specific competition occurs between two plant communities that share a border (Wilson and Agnew 1992; Adema et al. 2002). This hypothesis seems to explain the mechanisms of the boundary formation. Abrupt boundaries between herbaceous clonal plants are formed by inter-specific competition in a freshwater shoreline (Shipley et al. 1991). A clonal herbaceous plant, reed, often develops abrupt boundaries by creating a shady understory that excludes competitors (Keddy 2000). Those clonal plants created favorable environments for own species, and thus overcame most com-

petitors within areas where they establish. Not only herbaceous clonal plants but also woody non-clonal plants, i.e. *Picea glehnii* and *Alnus japonica* presented here, could create the selfish environments and inhibit natural afforestation of another species each other. In conclusion, the abrupt boundary can be controlled by chemical environment (particularly nutrient status and soil pH) rather than by physical factors (such as disturbances, topography or water level).

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References

Adema EB., Grootjans AP, Petersen J, Grijpstra J. 2002. Alternative stable states in a wet calcareous dune slack in The Netherlands. *Journal of Vegetation Science*, **13**: 107–114.

Cantu Silva I, Gonzalez Rodriguez H. 2001. Interception loss, throughfall and stem flow chemistry in pine and oak forests in northeastern Mexico. *Tree Physiology*, **21**: 1009–1013.

Duncan, RP. 1993. Flood disturbance and the coexistence of species in a lowland Podocarp forest, south Westland. *New Zealand Journal of Ecology* , **81**: 403–416.

Delcourt, PA, Delcourt, HR. 1992. Ecotone dynamics in space and time. In: A.J. Hansen, F. de Castri (eds), Landscape boundaries. Consequences for biotic diversity and ecological flows. New York: Springer-Verlag , pp. 19–54.

di Castri F, Hansen A. 1992. The environment and development crises as determinants of landscape dynamics. In: A.J. Hansen, F. de Castri (eds), Landscape boundaries. Consequences for biotic diversity and ecological flows. New York: Springer-Verlag, pp. 3–18.

Gunnarsson U, Rydin H, Sjörs H. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlosbergs Stormosse, Central Sweden. *Journal of Vegetation Science*, **11**: 277–286.

Grace JB, Wetzel RG. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies. *American Naturalist*. **118**: 463−474.

Haraguchi A. 1992. Seasonal changes in redox property of peat and its relation to vegetation in a system of floating mat and pond. *Ecological Research*, **7**: 205−212.

Haraguchi A, Iyobe T, Nishijima H, Tomizawa H. 2003. Acid and sea-salt accumulation in coastal mires of a *Picea glehnii* forest in Ochiishi, eastern Hokkaido, Japan. *Wetlands* **23**: 229−235.

Haraguchi A, Shibasaki M, Noda M, Tomizawa H, Nishio F. 1999. Climatic factors influencing the tree-ring growth of *Alnus japonica* in Kiritapp Mire, northern Japan. *Wetlands* **19**: 100−105.

Haeussler S, Tappeiner JCI. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). *Canadian Journal of Forest Research* **23**: 1487−1491.

Hobbs ER. 1986. Characterizing the boundary between California annual grassland and coastal sage scrub with differential profiles. *Vegetatio* **65**: 115−126

Hotes S, Poschlod P, Sakai H, Inoue T. 2001. Vegetation, hydrology, and development of a coastal mire in Hokkaido, Japan, affected by flooding and tephra deposition. *Canadian Journal of Botany,* **79**:341−361.

Keddy PA. 2000. Wetland ecology: Principles and conservation. Cambridge: Cambridge University Press, 614 pp.

Nakamura F, Jitsu M, Kameyama S, Mizugaki S. 2002. Changes in riparian forests in the Kushiro mire, Japan, associated with stream channelization. *River Research and Applications*, **18**:65−79.

Nanayama F, Satake K, Furukawa R, Shimokawa K, Atwater BF, Shigeno K, Yamaki S. 2003. Unusually large earthquakes inferred from tsunami deposits along the Kuril trench. *Nature*, **424**:660−664.

Parker GG. 1983. Throughfall and stemflow in the forest nutrient cycle. *Advances in Ecological Research*, **13**: 57−133.

Pennings SC, Callaway RM. 1992. Salt marsh plant zonation: The relative importance of competition and physical factors. *Ecology,* **73**: 681−690.

Richards MB, Stock WD, Cowling RM. 1997. Soil nutrient dynamics and community boundaries in the Fynbos vegetation of South Africa. *Plant Ecology*, **130**: 143−153.

Roberts J, Ludwig JA. 1991. Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray. *Australian Journal of Ecology*, **79**:117−127.

Saura-Mas S, Lloret F. 2005. Wind effects on dispersal patterns of the invasive alien *Cortaderia selloana* in Mediterranean wetlands. *Acta Oecologica,* **27**: 129−133.

Shipley B, Keddy PA, Lefkovitch LP. 1991. Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. *Canadian Journal of Botany,* **69**: 1420−1424.

Titus JH. 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. *Bulletin of Torrey Botanical Club* **117**: 429−437.

Tomizawa H, Oikawa M, Nishio F, Haraguchi A. 1997. Chemical modification of rain water by *Alnus japonica* wetland forest in Kiritapp Mire, Eastern Hokkaido, Japan. *Journal of Forest Research,* **2**:189−192.

Tsuyuzaki S, Haraguchi A, Kanda F. 2004. Effects of scale-dependent factors on herbaceous vegetation patterns in a wetland, northern Japan, with reference to water depth. *Ecological Research,* **19**: 349−355.

Tsuyuzaki S, Titus JH, del Moral R. 1997. Seedling establishment patterns in the Pumice Plains, Mount St. Helens, Washington. *Journal of Vegetation Science*, **8**: 727−734.

Veblen TT. 1985. Stand dynamics in Chilean Nothofagus forests. In: S.T.A. Pickett, P.S. White (eds), The ecology of natural disturbance and patch dynamics. Academic Press, Orland, pp. 35−51.

Vitt DH, Chee W. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio,* **89**: 87−106.

Walker LR, Chapin III FS. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*, **67**:1508−1523.

Wolejko L, Ito K. 1986. Mires of Japan in relation to mire zones, volcanic activity and water chemistry. *Japanese Journal of Ecology,* **35**: 575−586.

White PS, Pickett, STA. 1985. Natural disturbance and patch dynamics: an introduction. In: S.T.A. Pickett, P.S. White (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orland, pp. 3−13.

Wilson JB, Agnew ADQ. 1992. Positive-feedback Switches in Plant Communities. *Advances in Ecological Research*, **23**: 263–336.